DOI: 10.1007/s11099-011-0016-0 PHOTOSYNTHETICA 49 (1): 112-118, 2011

A comparative analysis of photosynthetic characteristics of hulless barley at two altitudes on the Tibetan Plateau

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Abstract

To determine the photosynthetic characteristics of C_3 plants and their sensitivity to CO_2 at different altitudes on the Tibetan Plateau, hulless barley (*Hordeum vulgare* L. ssp. *vulgare*) was grown at altitudes of 4,333 m and 3,688 m. Using gas-exchange measurements, photosynthetic parameters were simulated, including the maximum net photosynthesis (P_{max}) and the apparent quantum efficiency (α). Plants growing at higher altitude had higher net photosynthetic rates (P_N), photosynthesis parameters (P_{max} and α) and sensitivities to CO_2 enhancement than plants growing at lower altitude on the Tibetan Plateau. The enhancements of P_N, P_{max}, and α for plants growing at higher altitude, corresponding with 10 μmol(CO_2) mol^{-1} increments, were approximately 0.20~0.45%, 0.05~0.20% and 0.12~0.36% greater, respectively, than for plants growing at lower altitude, respectively, where CO_2 levels rose from 10 to 170 μmol(CO_2) mol^{-1}. Therefore, on the Tibetan Plateau, the changes in the photosynthetic capacities and the photosynthetic sensitivities to CO_2 observed in the C_3 plants grown above 3,688 m are likely to increase with altitude despite the decreasing CO_2 partial pressure.

Additional key words: altitude; apparent quantum efficiency; maximum net photosynthesis; Tibetan Plateau.

Introduction

In general, it has been assumed that a low CO_2 partial pressure has a negative effect on photosynthesis at high altitudes (Tranquillini 1964, Gale 1972, Friend and Woodward 1990, Sakata and Yokoi 2002). However, several observations have suggested that alpine plants have a higher photosynthetic capacity than lowland plants (Billings and Mooney 1968, Körner and Diemer 1987, Körner and Pelaez Menendez-Riedl 1990, Friend and Woodward 1990, Vats 2009). Studying the photosynthetic capacity of plants at different altitudes, Körner *et al.* found that the photosynthetic capacities of plants in the Alps at 2,600 m were 20% higher than those at 600 m (Körner and Diemer 1987, Körner and Pelaez Menendez-Riedl 1990). They suggested that this could be caused by pressure-related changes when the partial pressure of CO_2 decreases. These changes are caused by low-pressure air, which allows CO_2 to diffuse more quickly through the stomata and intercellular spaces of leaves (Körner and Diemer 1987, Körner 2003). Thus, RuBP oxygenase activity is reduced because of low O_2, which reduces photorespiration (Körner 2003), and this reduction could offset the suppression of photosynthesis due to low CO_2 levels. Therefore, along an altitudinal gradient, some relationship should exist between the difference of the photosynthetic capacities of plants and CO_2 partial pressure. However, these relationships would probably break down in cases where CO_2 partial pressure and temperature change with altitude. To predict the effects on the photosynthetic responses of plants at different altitudes due to changes in CO_2 partial pressure under global climate changes, a comparative study at different altitudes was employed.

Received 19 September 2010, *accepted* 24 January 2011.

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Abbreviations: C_i – intercellular CO_2 concentration; P_{max} – maximum net photosynthesis; P_{max350} – maximum net photosynthesis at 350 μmol(CO_2) mol^{-1}; P_N – net photosynthetic rate; PPFD – incident photosynthetic photon flux density; R_D – day respiration rate; T – leaf temperature; α – apparent quantum efficiency; $α_0$ – apparent maximum quantum efficiency; τ – CO_2 compensation point in the absence of day respiration; θ – convexity; SD – standard deviation.

Acknowledgements: This work was supported by the National Natural Science Foundation of China (30600085), the Major Basic Research Development Program of China (2010CB951704), the Knowledge Innovation Program of the Chinese Academy of Sciences (Kscx2-kw-n-44) and National Scientific and Technological Support Projects (2006BAC01A04).

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Many scientists have studied characteristics of plant photosynthesis at different altitudes and found that there are significant differences in the photosynthetic characteristics of alpine plants growing at different altitudes (Gale 1972, Kao and Chang 2001, Zhang *et al.* 2005, Castrillo 2006). However, almost all prior studies ignored the differences in the plant species, soil water, soil fertility, and other factors that occurred at different altitudes. These factors would probably influence the effect of CO_2 on plant photosynthesis. Hence, their findings could not adequately determine whether the differences in the photosynthetic characteristics of plants at different altitudes are caused by climatic factors that change with altitude. Furthermore, it is difficult to define photosynthetic sensitivity to CO_2 concentration changes at different altitudes.

The Tibetan Plateau is known as one of the most sensitive regions to global climate change, and it has an average elevation exceeding 4,000 m (Shi *et al.* 2006). Climatic factors present within particular biomes are diverse and complicated along an altitude gradient. Low CO_2 partial pressure due to high altitude is a unique alpine climate characteristic that makes it fundamentally different than the lowland climate, and alpine plants are more sensitive to climate change (Li and Tang 1988, Shi *et al.* 2006). Therefore, this region provides an ideal experimental situation for comparative research involving photosynthesis along an altitudinal gradient. To determine the characteristics of the photosynthetic responses of alpine plants in relation to alpine climate change, we analyzed the photosynthetic parameters of leaves from hulless baley, which are C_3 plants growing at different altitudes on the Tibetan Plateau, with special attention to the sensitivities of the dependencies of photosynthesis on CO_2 concentrations. Hulless barley was chosen to determine how differences in the dependencies and sensitivities to climatic factors change at different altitudes. The hulless barley was planted in pots at altitudes of 3,688 m and 4,333 m with the same soil and water-fertilizer management regimes. Using the measurements of leaf-level photosynthesis and a model describing light dependencies of leaf-level photosynthesis, two photosynthetic parameters, α and $P_{\max}$, were modelled; comparative P_N, α, and $P_{\max}$ characteristics and their relationships with leaf temperature at two altitudes on the Tibetan Plateau were analyzed. Finally, the sensitivities of these three parameters to CO_2 enrichment were further analyzed.

Materials and methods

Measurement site and experimental treatment: This research was conducted at two altitudes, 3,688 m at the Lhasa River valley (situated on the Lhasa Agricultural Experiment Station, Chinese Academy of Sciences in Tibet, 29°40′40″N, 91°20′37″E) and 4,333 m near the south edge of the Nyainqntanglha Mountains (situated approximately 1 km from Damxung county, Tibet municipality, China, 30°25′N, 91°05′E). Both sites belong to the semiarid temperate plateau monsoon climate zone. The mean daily air temperatures during the growing season and annual mean precipitation are 17°C and 425 mm at 3,688 m, respectively, while they are 15°C and 475.8 mm at 4,333 m. The vegetation is dominated by crops and by *Tipa capillacea*, *Carex montis-everestii* and *Kobresia pygmaea* at 3,688 m and 4,333 m, respectively (Xu *et al.* 2007). The soil types are shrubby meadow soil at the 3,688 m and alpine meadow soil at 4,333 m.

Hulless barley, a C_3 crop cultivated widely on the Tibetan Plateau, was selected for this study. Seeds were sown in May of 2008 at both measurement sites in pots 20 cm in diameter and 30 cm high. Three to four seeds were sown per pot, and 15~20 pots were set up at each study altitude. To minimize the effects of soil properties, the shrubby meadow soil was selected from the 3,688 site, which has a 2% of organic matter content, consisting of 0.084–0.103% total nitrogen and 0.015–0.026% total phosphorus. The plants were well watered to a water content of 70–80% of field capacity and fertilized with N and P [0.471 g(N) and 0.236 g(P_2O_5) per pot during the experiment] to ensure that possible acclimations to the alpine climate were unrelated to water and nutrient stress. Plants grew in open habitats. Because of the acclimations of growth rates to temperatures, the emerging times for flag leaves were different between the two altitudes (late June at 3,688 m and mid-August at 4,333 m). When the youngest flag leaves were 2~3 cm long after 3-day outgrowth, well developed leaves were selected and marked with labels. These treatments allowed us to avoid the influence of flag leaf age on photosynthetic capacity.

Gas exchange was measured using a portable photosynthesis system (*LI-6400, LI-COR, Inc.*, Lincoln, NE, USA) with a 3 cm × 2 cm (length × width) leaf chamber. Prior to the measurements, photosynthesis was induced by exposing leaves to sunlight for approximately one hour. The measurements were conducted on fully expanded flag leaves. The flag leaves had an age of full expansion on plants of up to 6~8 days, an average length of 7~8 cm. The upper section of each leaf was enclosed in the chamber at a distance of 2.5~3.0 cm away from the blade and measured with a vernier caliper.

The response of CO_2 assimilation to light intensity was measured using the regression of the photosynthetic photon flux density (PPFD) from 2,200 $\mu mol\ m^{-2}\ s^{-1}$ to 0 $\mu mol\ m^{-2}\ s^{-1}$ with an *LI-6400-02B* red (680 nm)/blue (430 nm) light source in the sensor head, with a native CO_2 concentration of approximately 400 ± 5 $\mu mol(CO_2)\ mol^{-1}$ at 3,688 m and 375±5 $\mu mol(CO_2)\ mol^{-1}$ at 4,333 m and leaf temperatures of 15, 20, 25, and 30°C. The leaf temperature control simulated the ambient air temperature conditions, and temperature anomalies were less than 5°C. To prevent stomatal closure which would decrease photosynthesis, the vapour pressure deficit around the leaf in the chamber was maintained at between 0.5 and 1.0 kPa during measurements.

To determine the differences of the CO_2 dependencies of photosynthetic capacity between altitudes, additional curves were measured in leaves from the CO_2 treatments under conditions of light saturation at 1,600 μmol m^{-2} s^{-1} and a leaf temperature of 20°C. The CO_2 concentration of the chamber air was reduced stepwise from 400 μmol(CO_2) mol^{-1} to 0 μmol(CO_2) mol^{-1} and then increased stepwise from 0 μmol(CO_2) mol^{-1} to 1,300 μmol(CO_2) mol^{-1} by the injection of CO_2 under the control of an infrared CO_2 analyzer. It usually took 200~300 s for gas-exchange rates to stabilize after changing the light density and CO_2 concentration. Afterward, gas-exchange measurements were recorded.

Such plots of net photosynthetic rates (P_N) as a functions of CO_2 and incident light levels were made continuously on several clear days between 09:00–18:00 and 09:30–10:30 on 4~6 leaves per temperature range at each site. From these data, three curves from each altitude at 15, 20, 25, and 30°C were selected to analyze and simulate the photosynthetic characteristics of hulless barley.

Model description: The nonrectangular hyperbola model that was proposed to describe the relationship between PPFD and the rate of photosynthesis is expressed as (Marshall and Biscoe 1980):

$$P_N = \frac{\alpha \cdot \mathrm{PPFD} + P_{max} - \sqrt{2(\alpha \cdot \mathrm{PPFD} + P_{max}) - 4\alpha P_{max}\theta}}{2\theta} - R_D \tag{1}$$

where P_{max} and α are the maximum net photosynthesis and the apparent quantum efficiency, respectively. R_D is day respiration rate other than photorespiration, PPFD is the incident photosynthetic photon flux density, and θ is the apparent convexity at the shoulder of the photosynthetic light-response curve ($0<\theta<1$). The two parameters P_{max} and α can be simulated from the equation of the photosynthetic light responses.

To find the CO_2 dependencies of P_{max} and α, the two functions proposed by Gaastra *et al.* (1994) and Goudriaan *et al.* (1985) are as follows:

$$\alpha = \alpha_0 \frac{C_i - \tau}{C_i + 2\tau} \tag{2}$$

$$P_{max350} = \frac{C_i - \tau}{350 - \tau} \times P_{350} \tag{3}$$

where P_{max350} and α_0 are the maximum net photosynthesis at 350 μmol(CO_2) mol^{-1} and the apparent maximum quantum efficiency, respectively, and τ and C_i are the CO_2 compensation point in the absence of day respiration and the intercellular CO_2 concentration, respectively. P_{350} is the net photosynthesis at 350 μmol(CO_2) mol^{-1}. Factor τ, which varied with leaf temperature (T), was expressed as follows (Brooks and Farquhar 1985):

$$\tau = 42.7 + 1.68\ (\mathrm{T} - 25\ ) + 0.012\ (\mathrm{T} - 25)^2 \tag{4}$$

P_{max350} and α_0 can be inverted based on Eq. 2, Eq. 3 and Eq. 4, with P_{max} , α, τ, and C_i as inputs, respectively. As parameters of photosynthetic capacity, P_{max350} and α_0 should be rather stable for a specific stand independent of temperature and CO_2 concentration. Therefore, it is possible to estimate values for P_{max} and α at a given CO_2 concentration.

Model-fitting techniques and statistical analysis: The data were processed with *Origin 8.0* software (*OriginLab Corp.*, Northampton, MA, USA).Nonlinear least-squares fitted to Eq. 1, Eq. 2 and Eq. 3 and iterations for P_{max}, α, α_0, and P_{max350} were applied. One-way analysis of variance (ANOVA) was applied to assess differences in the net rates of photosynthesis and photosynthetic parameters between plants at the two altitudes.

Results

Response of photosynthesis to irradiance: Curves relating native P_N to irradiance for fully expanded flag leaves of hulless barley were fit for two altitudes with leaf temperatures set at 15°C, 20°C, 25°C and 30°C and the native CO_2 concentration in the field (Fig. 1). At the two sites, net photosynthesis rapidly increased at a rate of 0~200 μmol m^{-2} s^{-1}. Subsequently, the rates slowly increased by 400~1,000 μmol m^{-2} s^{-1} and peaked at approximately 1,500~1,700 μmol m^{-2} s^{-1}. The net photosynthetic rates showed significant differences over a range of leaf temperatures, including 15°C, 20°C, 25°C and 30°C, and the nearly optimum temperature was 20°C.

Hulless barley grown at 4,333 m had higher rates of net photosynthesis than that grown at 3,688 m over all measurements at a given leaf temperature ($p<0.05$). Plants from 4,333 m exhibited the light-saturated rate of 23 μmol(CO_2) m^{-2} s^{-1}, which is approximately 2.5 μmol(CO_2) m^{-2} s^{-1} over the light-saturated rate at 3,688 m under a saturated light intensity of 1,600 μmol m^{-2} s^{-1} and optimum leaf temperature of 20°C.

Parameters of α and P_{max}: To assess the responses of biochemical photosynthetic properties to light, α and P_{max} were two key parameters used to characterize the status of the leaf photosynthetic apparatus (Marshall and Biscoe 1980). The native parameters of α and P_{max} for each of

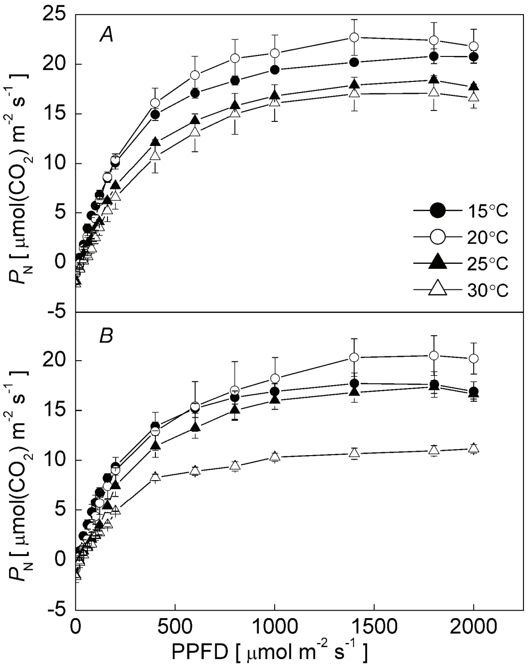

Fig. 1. Net photosynthetic light-response curves for fully expanded flag leaves of hulless barley. The curves were fit from representative hulless barley growing at *A*: 4,333 m and *B*: 3,688 m with leaf temperatures of 15°C, 20°C, 25°C and 30°C. Each symbol represents the mean value of three replications and the standard deviation (± SD) was also determined.

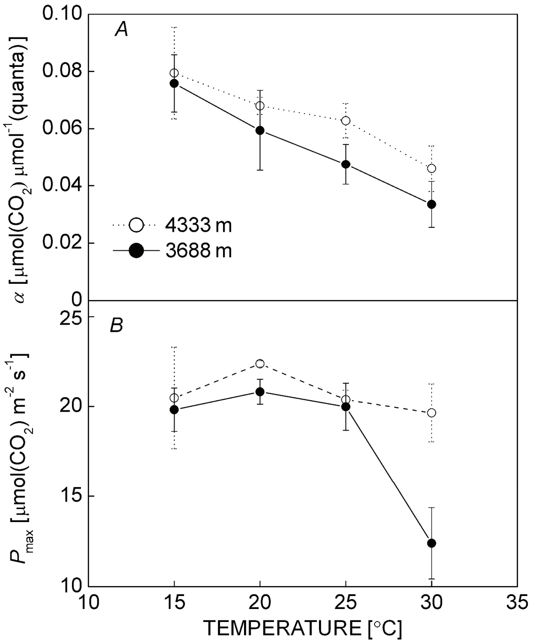

Fig. 2. The relationship between apparent quantum efficiency (α) and *A*: leaf temperature or *B*: maximum net photosynthesis (P_{max}) at 4,333 m and 3,688 m. Each symbol represents the mean value of three replications and the standard deviation (± SD) was also determined.

the leaves were separately estimated using a nonlinear least-squares method and the photosynthetic light measurements mentioned above to iterate Eq. 1. When the measured P_N and that fitted in Eq. 1 were within 0.01 μmol(CO$_2$) m^{-2} s^{-1}, the iteration was concluded. The values of α and P_{max} are shown in Fig. 2.

In Fig. 2*A*, declining trends in α with increasing leaf temperatures were observed for the two altitudinal treatments. The α value declined from 0.0794 to 0.0460 at the altitude of 4,333 m and from 0.0759 to 0.0335 at the altitude of 3,688 m when leaf temperatures increased from 15°C to 30°C. However, there were significant differences in α among the two groups of plants ($p<0.05$). Higher-altitude plants tended to have higher α values than lower-altitude plants with a mean difference of 17.2% for all leaf temperatures, and the greatest difference was 27.18% at 30°C. To minimize the variation in the photon efficiency in response to leaf temperature, α_0 for the two altitudes was determined using Eq. 2. The α_0 at 4,333 m and 3,688 m was 0.098 and 0.081, respectively, which meant that plants growing at the higher altitude had higher light utilization efficiencies than plants growing at the lower altitude.

From Fig. 2*B*, we can see that the variation patterns of P_{max} are highly similar at the two altitudes, as characterized by an initial rise and subsequent decline. They reached a maximum of approximately 22.37 μmol(CO$_2$) m^{-2} s^{-1} at the higher altitude and 20.81 μmol(CO$_2$) m^{-2} s^{-1} at the lower altitude at nearly the same leaf temperature, approximately 20°C. The leaf temperature sensitivities of P_{max} did not differ significantly between the two altitudes ($p>0.05$). However, there were slight fluctuations in P_{max} with an average fluctuation of 1.54 μmol(CO$_2$) m^{-2} s^{-1} per leaf temperature in plants growing at 4,333 m, while the average fluctuation was 3.14 μmol(CO$_2$) m^{-2} s^{-1} in plants growing at 3,688 m. Despite not being significant ($p>0.05$), the average difference in P_{max} between the two altitudes was about 11.84%. To avoid the influence of different CO$_2$ concentrations between the two altitudes on the photosynthetic rate (Barigah *et al* 1994), P_{max350} values were calculated using Eq. (3). Similar to the previous calculation, P_{max350} was apparently higher at 4,333 m than at 3,688 m, corresponding to 29.14 μmol(CO$_2$) m^{-2} s^{-1} and 23.68 μmol(CO$_2$) m^{-2} s^{-1}, respectively.

Sensitivities of photosynthesis to CO$_2$ for the two altitudes: To intuitively describe the sensitivities of photosynthesis to CO$_2$ in C$_3$ plants growing at the different altitudes on the Tibetan Plateau, curves relating P_N to C_i were obtained from flag leaves of hulless barley from each altitude treatment under a saturated PPFD of 1,600 μmol m^{-2} s^{-1} and a leaf temperature of 20°C. The responses of P_N to elevated CO$_2$ are shown in Fig. 3 for the plants at the two altitudes. P_N for the plants at 4,333 m was higher than for those at 3,688 m under

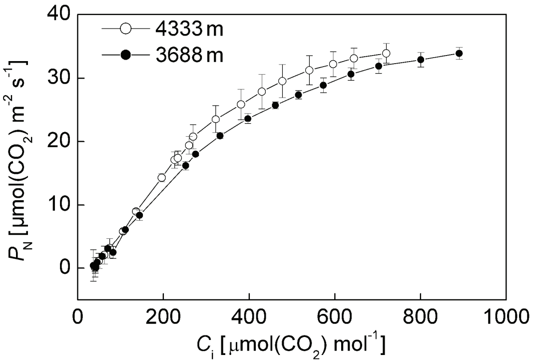

Fig. 3. Correlations between net photosynthetic rate (P_N) *vs.* intercellular CO_2 concentration (C_i) response measured for native hulless barley at 4,333 m and 3,688 m at an incident photosynthetic photon flux density (PPFD) of 1,600 μmol m^{-2} s^{-1} and leaf temperature of 20°C. Each symbol represents the mean value of three replications and the standard deviation (± SD) was also determined.

elevated CO_2 ($p<0.05$), and the shapes of the P_N/C_i curves were slightly different between the two altitudes. This discrepancy indicated that the sensitivities of photosynthesis to elevated CO_2 were different at the two altitudes.

α, P_{max}, and P_N were calculated using Eq. 2, Eq. 4 and Eq. 1 with P_{max350} and α input at a 10 μmol(CO_2) mol^{-1} progressive enhancement of intercellular CO_2 for both altitudes, a PPFD of 1,600 μmol m^{-2} s^{-1} and a leaf temperature of 20°C. α, P_{max} and P_N increased with increasing CO_2 by 0.4~1.5%, 2.4~4.4% and 2.3~4.6% per 10 μmol(CO_2) mol^{-1} elevated CO_2, respectively (Fig. 4). However, α, P_{max}, and P_N for the higher altitude plants were more sensitive to CO_2 treatment, showing levels that were 0.12~0.36%, 0.05~0.20% and 0.2~0.45% higher than for the lower altitude plants, respectively. In addition, the percentage of enhancement of α, P_{max}, and P_N decreased with additional CO_2 increments up to 170 μmol(CO_2) mol^{-1}. When CO_2 was above 170 μmol(CO_2) mol^{-1}, the changes and differences between the two altitudes in the percentage of enhancement were small.

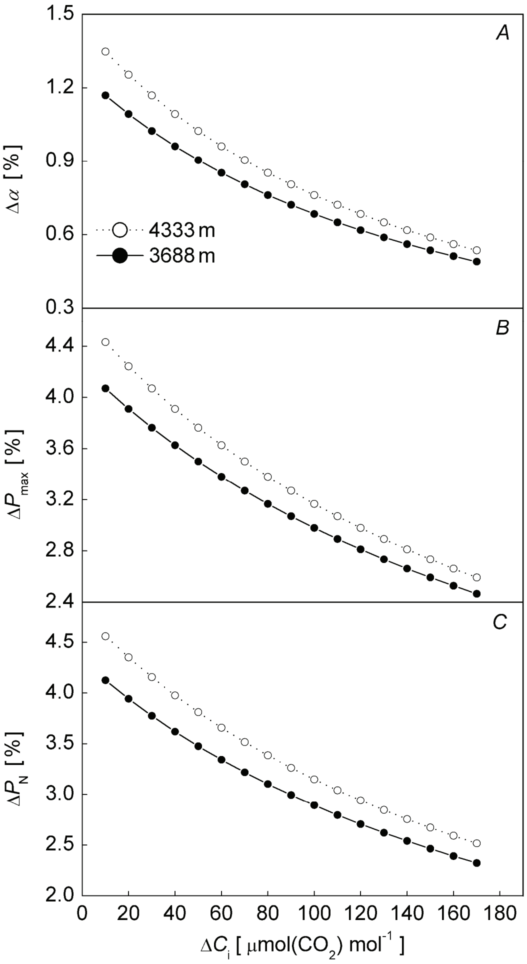

Fig. 4. Estimates of enhancement percentages of apparent quantum efficiency (α), maximum net photosynthesis (P_{max}) and net photosynthetic rate (P_N) plotted as a function of 10 μmol mol^{-1} progressive enhancement of intercellular CO_2 from 0 to 170 μmol mol^{-1}. These parameters were obtained for native hulless barley at 4,333 m and 3,688 m at incident photosynthetic photon flux density (PPFD) of 1,600 μmol m^{-2} s^{-1} and leaf temperature of 20°C.

Discussion

In this study, we compared the net photosynthetic rate and photosynthetic parameters for flag leaves of hulless barley growing at 3,688 m and 4,333 m on the Tibetan Plateau. Upward regulation of photosynthetic capacity has been characterized in plants with increasing altitudes. This result is consistent with the reported data from Körner *et al.* (2003). However, some studies on altitudinal trends in photosynthetic capacities offered conclusions that contradict our study (Badger 1985, Heber and Walker 1992, Cabrera *et al.* 1998, Kao and Chang 2001, Zhang *et al.* 2005). These contradictions could be explained by a decrease in photosynthesis with altitude due to lower leaf N content, water stress and lagging leaf maturity, which are caused by decreasing soil N fertilization, precipitation, and growth temperature with altitude. In our experiment, these constraining factors on photosynthesis were avoided by pot planting, uniform water-fertilizer management and the labeling of flag-leaf ages at the two altitudes. The primary reason for the greater photosynthetic capacity of plants at higher altitude is that the reduction in RuBP carboxylation is less than the reduction in RuBP oxygenation with increasing altitudes, which causes much less of a reduction in photosynthesis compared to that observed during photorespiration in alpine plants in the alpine environment of the Tibetan Plateau (Terashima *et al.* 1995). In addition, photosynthetic proteins (Körner *et al.* 1989, Morecroft and Woodward 1996, Pyankov *et al.* 1999), stomatal density (Körner *et al.* 1986), rate of gas diffusion (Gale 1972) and the activities of photosynthetic enzymes (Castrillo 2006) in the leaves of alpine plants have been shown to increase with increasing altitudes (Körner *et al.* 1989), all of which correlate with photosynthetic acclimation to the climatic conditions of low air pressure, cool temperature (Körner 2007), and high irradiation (Oguchi *et al.* 2003). Indeed, those positive effects could overcome the negative effect of decreasing CO_2 partial pressure with increasing altitudes in an alpine environment.

For alpine plants, the optimum temperature for photosynthesis decreased with increasing altitudes (Dillaway 2009, Fryer and Ledig 1972, Berry and Bjorkman 1980, Rada *et al.* 2010). In our study, the optimum photosynthetic temperature was about 20°C, lower than the 25°C optimum that has been measured for lowland plants (Akhkha *et al.* 2001). The photosynthetic capacity decreased as the temperature increased to a level above the optimal value (Lindroth *et al.* 1998). Moreover, the photosynthetic abilities (P_N) of plants growing in cool climates were more sensitive to temperature increases than those of plants growing in warm climates when the temperature was over the optimum (Tranquillini *et al.* 1986). Therefore, the decreases of photosynthetic capacities at high altitude were greater than those at low altitude when temperatures increased up to over 25°C. Taking this into account, the lower photosynthetic capacities observed for plants at high altitude compared to those at low altitude at 30°C (Zhang *et al.* 1992, Liu *et al.* 2000, Shi *et al.* 2004) may be explained.

Our quantitative estimates of CO_2 sensitivity were modelled according to the light response and CO_2 dependency models of α and P_{max}. These models were proposed on the basis of the physiological characteristics of photosynthesis (Farquhar *et al.* 1980, Marshall and Biscoe 1980, Goudriaan *et al.* 1985) and experimentally confirmed to be reasonable (Moreno-Sotomayo *et al.* 2002, Pons and Anten 2004, Zhou *et al.* 2010). According to the parameters estimated from these models, we were able to determine that plants at the higher altitude had higher photosynthetic sensitivities to CO_2 increases than plants at the lower altitude. It can be predicted that the net photosynthetic rate for hulless barley growing at 4,333 m and 3,688 m would increase by 26.9% and 16.3%, respectively, under the atmospheric CO_2 (C_a) increases of up to 458 $\mu mol(CO_2)\ mol^{-1}$ that are predicted for 2050 (McMichael *et al.* 2004), when the constant C_i/C_a ratio is assumed to be 0.7 with a temperature of 20°C (Weber *et al.* 985, Cannon and Roberts 1995).

In summary, C_3 plants native to an alpine environment and characterized by low atmospheric pressure and low temperature have higher photosynthetic capacities and photosynthetic sensitivities to CO_2 concentration changes at higher altitude than at lower altitude on the Tibetan Plateau, while CO_2 partial pressure decreases with altitude.

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